CONIFEROUS POLLEN TYPES OF THE SOUTHERN HEMISPHERE, I. ABERRATION IN ACMOPYLE AND PODOCARPUS DACRYDIOIDES

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IN COMPARING THE POLLEN GRAINS of the Podocarpaceae with those of the Pinaceae, Mme. van Campo (1950) has recognized their common and very ancient source. In this view she has followed Prof. R. Florin (1936), who has shown how very closely aberrant grains of members of both families may approach ones normal to the Cordaitales. It is his opinion that the morphological affinity with the extinct group is strongest in the grains of certain genera of the Pinaceae. Van Campo considers that the Podocarpaceae may prove to be older, however, and points to the divergent groups persisting today. Further, she admits difficulty in deciding to which family certain types belong.

Sir Albert C. Seward (1914) ran into the same difficulty in identifying the first gymnospermous grains discovered in Antarctic deposits. He set up and defended his organ-genus *Pityosporites* in the belief that it represented abietineous grains, but soon decided that it was most probably based on podocarp material. Unfortunately, the name must be upheld as a catch-all for older bisaccate grains, of both hemispheres, which have characters common to the two families. However, as pollen studies proceed, closer identification of fossil with living types is made possible, so that a dwindling remnant of southern hemisphere "incertae" is likely to lodge, or remain, in *Pityosporites*.

Thus, despite evidence for relationship in the two major families, diagnostic differences do occur and could be exploited much more than at present for stratigraphical, distributional, and climatological studies. The work of Dr. Isabel C. Cookson, Dr. R. A. Couper, and Mr. Basil E. Balme, to mention only some who have worked in both hemispheres, is outstanding in this respect.

Particular weakness still lies in our lack of detailed knowledge of *Pinus* pollen, as contrasted with that of *Podocarpus*, or of *Cedrus*, as opposed to some of the *Dacrydia*. Records of one or the other will crop up somewhat erratically in fossil work from either hemisphere until the position is clarified. For instance, a report on Lower Miocene deposits of Silesia by Prof. Stefan Macko (1957) presses identity of his conifer types with living podocarps such as *Podocarpus dacrydioides* A. Rich. and *Dacrydium cupressinum* Soland. ex Forst. f. While I am willing to admit that genera now represented in New Zealand may also have occurred in Eurasia, I feel sure that his photomicrographs and descriptions do not clinch the matter for two reasons: the reticulate sculpture rules out a *Dacrydium*, and the presence of *Crossotheca* spores in the same deposit suggests redeposition from older beds for the "*Podocarpus*," if closer affinity with known three-sac types cannot be proved. Neither set of microfossils exemplified by Macko comes any closer to Miocene antecedents of these species as we know them from New Zealand deposits. I mention these examples in order to stress the difficulties involved in comparing fossil podocarps of the two hemispheres, rather than to detract from Prof. Macko's main theme, which is the very real affinity between the Tethyan (or Poltavian) part of his microflora and that of Indo-Malayan vegetation of today.

Few still believe that *Pinus* and its close allies ever reached far into the Southern Hemisphere: *Pinus* today stops short in the West Indies and Guatemala, on one side of the world, and in the Sunda Islands, less than six degrees south of the Equator, on the other. On the other hand, some podocarps are found far above the Equator, mainly in the wet highlands of Central America, of Nepal, the Philippines, China, the Ryukuyu Islands, and Japan.

We are indebted to Dr. R. Florin, particularly, for purging the records, living and fossil. For South America, Antarctica, and New Zealand he has shown, for instance, that all the "Sequoia" records are false, and he has usually been able to place the macrofossils on which they were based in *Podocarpus* or *Acmopyle*.

Microfossil records usually lag behind those for macrofossils, and this is true for *Acmopyle*, one of the rarest of living conifers. Two living species, *A. pancheri* Pilg. and the very closely allied *A. alba* Buchholz, are known from the high serpentine areas of eastern New Caledonia (see Chevalier, 1957), and a third, *A. sahniana* Buchholz & N. E. Gray, from Fiji. Florin's ancient species, based on leaves and twigs, are *A. antarctica* from Seymour Island, Graham Land (Oligocene or Lower Miocene) * and *A. engelhardtii* (Eocene) from Río Pichileufu in Argentina.

An excellent note on the habitat and rich assemblage of conifers associated with *Acmopyle* is given for New Caledonia by Compton (1922). There, at 3000 ft. above sea level, the generic mixture and the ecological conditions must be very similar to those at a slightly lower altitude on Mount Te Moehau, an isolated "island," untouched by glaciation, on the Coromandel Peninsula about 40 miles east of Auckland, New Zealand. In both areas the relict forest seems to survive, as Compton puts it, through "stubborn resistance," as it is out of equilibrium with its environment.

ABERRATION IN CONIFER POLLEN GRAINS

Various authors have dealt with normal pollen grains in the Podocarpaceae, but few have described the range of aberrance in this important group, or have tried to assess its importance. I shall, therefore, confine myself in this note to its occurrence in *Acmopyle pancheri* and

* The age of the Seymour Island sediments was given by Florin (1940) and others as Eocene: recent work by the Falkland Islands Dependencies Survey indicates, however, that there are no Eocene sediments left in the region.

Podocarpus dacrydioides and shall mention the normal form only where comparison is necessary.

Hybridism and unknown factors lead to many deviations in pollen grain morphology, disturbing the familiar face, or physiognomy, of a grain. It is as though a cheek were turned in the Coniferales, in particular, when grains gain or lose bladders, reveal ancestral markings, or remain fused back-to-back with four bladders instead of two. The change of profile, so to speak, now offers new clues to cell behavior and, perhaps, to evolutionary trends. In some, the differences seem to represent a recapitulation difficult to trace except in very young or aborted grains.

Among irregularities noted for these southern genera are trisaccate grains in the normally disaccate *Acmopyle* and grains with more or less confluent sacs (bladders) or with triradiate or slashlike scars on the cap (the proximal side of the grain) in *Podocarpus dacrydioides*. Sac fusions or abortions may also occur in *Dacrydium cupressinum* and in the New Zealand species of *Phyllocladus*.

In *Acmopyle* and *Podocarpus dacrydioides*, at least, hybridism does not seem to have been involved, as the species are geographically and genetically isolated. No hybrids have been reported from *Acmopyle* or from the *Dacrycarpus* section of *Podocarpus*. Further, the frequency of irregularity is quite low, about five per cent (of 300 grains studied; Cranwell, 1940) being noted in *Podocarpus dacrydioides* and under one per cent in *Acmopyle* (with 600 grains studied). Van Campo (1950), on the other hand, reports 100 per cent aberrance in certain hybrid *Tsuga* material she investigated.

It is worth noting that few conifer hybrids have been accepted for the southern hemisphere, the late Dr. H. H. Allan (1961) giving only two groups in *Flora of New Zealand*. Both were between species with disaccate grains. Hair (1958) and Hair and Beuzenberg (1958a,b) have confirmed one of these groups in their wide surveys of chromosome numbers in the Podocarpaceae. Their material was a cross of *Podocarpus hallii* Kirk × *P. nivalis* Hook. from the closely related "hallii-totara-nivalis" complex, and it yielded counts of $2n = 36$, while the parents yielded $2n = 34$ and 38 respectively. The authors stress the importance of the evidence for chromosome inconstancy discovered in many of the 52 species, and the one hybrid, they have studied. They state (1958b) that the Podocarpaceae, instead of displaying "the unvarying basic numbers of most families of slow-growing, long-lived" gymnosperms, shows "surprising variation . . . which points both to the past and to the future." Hair (1958) adds that this "chromosomal polymorphism" is "a surprising discovery amongst the long-lived woody plants generally." Their lists show that few species with high basic chromosome numbers have trisaccate grains either regularly or occasionally. Apart from *Microcachrys* and *Pherosphaera* this condition is strong only in the groups in which Hair and Beuzenberg have demonstrated a low basic number, e.g., 10 for *Acmopyle pancheri*, *Podocarpus dacrydioides* and *Dacrydium cupressinum* ($2n = 20$).

Only a few of the trisaccate species cross the Equator, one running north to the Philippines. All of these species belong to section *Dacrycarpus*, which has also a Chilean species described by Florin (1940) from fossil twigs. The discovery of more fossil material, as claimed by Macko (1957), would therefore represent a great extension of range for species with this pollen type. According to European reports, coniferous grains with more than two sacs are by no means common in northern deposits.

TRISACCATE GRAINS IN ACMOPYLE

The only illustrations of *Acmopyle* pollen grains to which I have had access are those of Erdtman and of Ueno. Dr. Erdtman illustrated the pollen of *A. pancheri* in 1957, promising to give the necessary text in his second volume on the gymnosperms, while Dr. Ueno gave an extremely small sketch for *A. alba* in 1960.

Thanks to Dr. Erdtman, I was permitted to see the slide on which his sketches were based; later I received fresh pollen cones from Dr. David de Laubenfels of Syracuse University, New York (*P 130*, collected on Mount Mou, New Caledonia, Oct. 9, 1957), and it was in this second collection that I noted the aberrant forms, which comprised under one per cent with three sacs and a small number only that were dwarfed, doubled, or slightly irregular in size of the sacs. The accompanying plate illustrates a trisaccate grain, together with two typical disaccate grains, seen in distal and lateral views (Figs. 1–3).

It should be noted that the three sacs are in perfect balance and condition (Fig. 1), but the exine of the corpus (body of the grain) is very thick and is embayed between the sacs. As in normal grains, the puffed bladders are attached by narrow bases and lie wholly on the distal surface of the grain.

Most of the irregular grains were smaller than the normal ones, but the overall measurement, with sacs included, was little smaller, being about 62μ. No grains were broken, but several (normal) had shed a sac very cleanly, possibly due to the rigors of acetolysis during the preparation of the sample. The tendency to shed seems stronger than in other podocarp pollen types: it may thus be significant that sacless grains of this type occur rather freely in Upper Cretaceous Antarctic sediments which I am studying at present. No bladders like those of *Acmopyle* have been recognized, however, although many fragments have persisted.

SOME FOSSIL OCCURRENCES OF TRISACCATE TYPES

Occurrences in older floras will not be discussed in detail here, but it is worth noting a second trisaccate type also found by the author in the Antarctic samples. Deviations from the coniferous types suggest that it may have been shed by a pteridosperm.

The trisaccate condition is certainly very old, though not as old, it seems, as some of the types with enveloping or cingulate sacs. In *Podocarpus dacrydioides*, at least among the podocarps, a deviant takes the form of this more ancient fused sac, comparable with those sometimes developed in *Pinus sylvestris*, according to reports by Eneroth (see Florin, 1936). Such grains occurring in podocarps, pines, and their allies, even if rarely, seem to give good support for Florin's views on the common ancestry of these groups in the Cordaitales.

Trisaccate grains occur rather sparingly among the Abietineae in both fossil and living material. They occurred also in extinct groups the affinities of which are little understood. Couper (1958) has reported them, for instance, in frequencies of one in a thousand for the normally bisaccate *Caytonanthus arberi* (Thomas) Harris, a member of the Caytoniales which lived in the Mesozoic period in Britain.

The nomenclature for these types is especially difficult: some are lumped in *Trisaccites*, or, if a comparatively recent origin is suspected, in an organ-genus suggesting affinity, e.g., *Podosporites*. Where there is a continuous record for a species, as for *Podocarpus dacrydioides* in New Zealand, the affinity can well be claimed, but even for this distinctive type the record does not yet go back beyond the Tertiary.

TRIRADIATE SCARS IN PODOCARPUS DACRYDIOIDES

The triradiate scar, the mark of contact with other grains of a developing tetrad, occurring always on the proximal or cap side, is rarely noted in conifers, and has never been confirmed for any angiosperm, although *Coprosma macrocarpa* Cheesem., for one, has a polar marking which mimics a scar. Wodehouse (1935) has illustrated a scar for *Abies nobilis* Lindl., for instance, and has stated that it is a "diagnostic character when found but it is generally very faint and difficult to see." Florin (1936) reports much the same thing for *Cordaiantkus* and illustrates a grain with a small, compact scar.

Ueno (1957) has given the only reports of a scar in *Podocarpus dacrydioides*, as far as I know. His illustration I noted with admiration and a mild chagrin, as I had never observed one of these scars in the many grains I have worked with, living or fossil; the only deviations I had seen were frillings and fusions of the sacs. I was fortunate, therefore, on October 25, 1958, to be able to collect young cones, which I took from a small tree, not long out of its juvenile stage, by the Waitakere Stream not far from Auckland. In this material I found an abundance of scars, as well as broad slash-like markings not mentioned by Dr. Ueno.

In *Podocarpus dacrydioides*, the scar lies in the middle of the body of the grain, sending its long, untapered arms out almost to the equator where each comes symmetrically and abruptly to a point. As will be seen (FIGS. 6, 7), the arms are broad, both margins and surfaces being clearly delimited. By comparison with such ancient types as *Illinites* Kosanke and *Fuldaesporites* Leschik (as illustrated in Potonié, 1958, *Taf. 7, 62* and *Taf. 9, 91*, respectively), or with modern fern types, such as the spores of *Adiantum*, this is a large and magnificent scar. It does not run into and fuse with the ridge encircling the equator, as Ueno reports for *Tsuga*. I agree with him, however, in his suggestion that only young grains are likely to show the triradiate marking to advantage.

IRREGULARLY SCARRED GRAINS

The chief aberrations in this species, and the ones most likely to be of importance, are the slash-like strips running singly on in pairs across the proximal surface. Their "selvage" margins are wide and calloused (FIGS. 9, 10) and thus suggest rigidity, rather than distensibility, of the wide and delicate membrane of the distal surface. This latter is usually spoken of as the "furrow," although it is not homologous with the furrow of most of the angiosperms.

Several fossil pollen genera are characterized by rather similar rifts (see Potonié, 1958, *Taf. 7, 63, 64*, and especially Balme and Hennelly, 1955). These are disaccate grains, the gashes tending as a rule to run straight and at right-angles to the side furrows on the other side of the grain. In *Podocarpus dacrydioides*, likewise, the seemingly haphazard pattern of rifts may be determined by the geography of a triangular, rather than an elongate, furrow area. In a "normal" young grain, the arms of the *perfect* triradiate scar will run toward the apex of each subtending air sac, as it would to the three angles formed on the amb of trilete fern spores. The disturbance of the abnormal grain, whatever its cause, may thus lead to gross thickenings and erratic trends in the trisaccate types.

In "Lueckisporites" of Balme and Hennelly (1955) a straight gash occurs together with lesser parallel striation. Such grains are especially important in members of the Gondwana Flora (see also Pant & Nautiyal, 1960) but have not yet been reported from Gondwana deposits in New Zealand. Their association with delicate triradiate crests in some sacless microspores described by the Australian workers suggests that their early function was separate from that of the scar. It will be interesting to discover for modern conifers what relationship the heavy gashes have to both the triradiate scar and the ancient striations.

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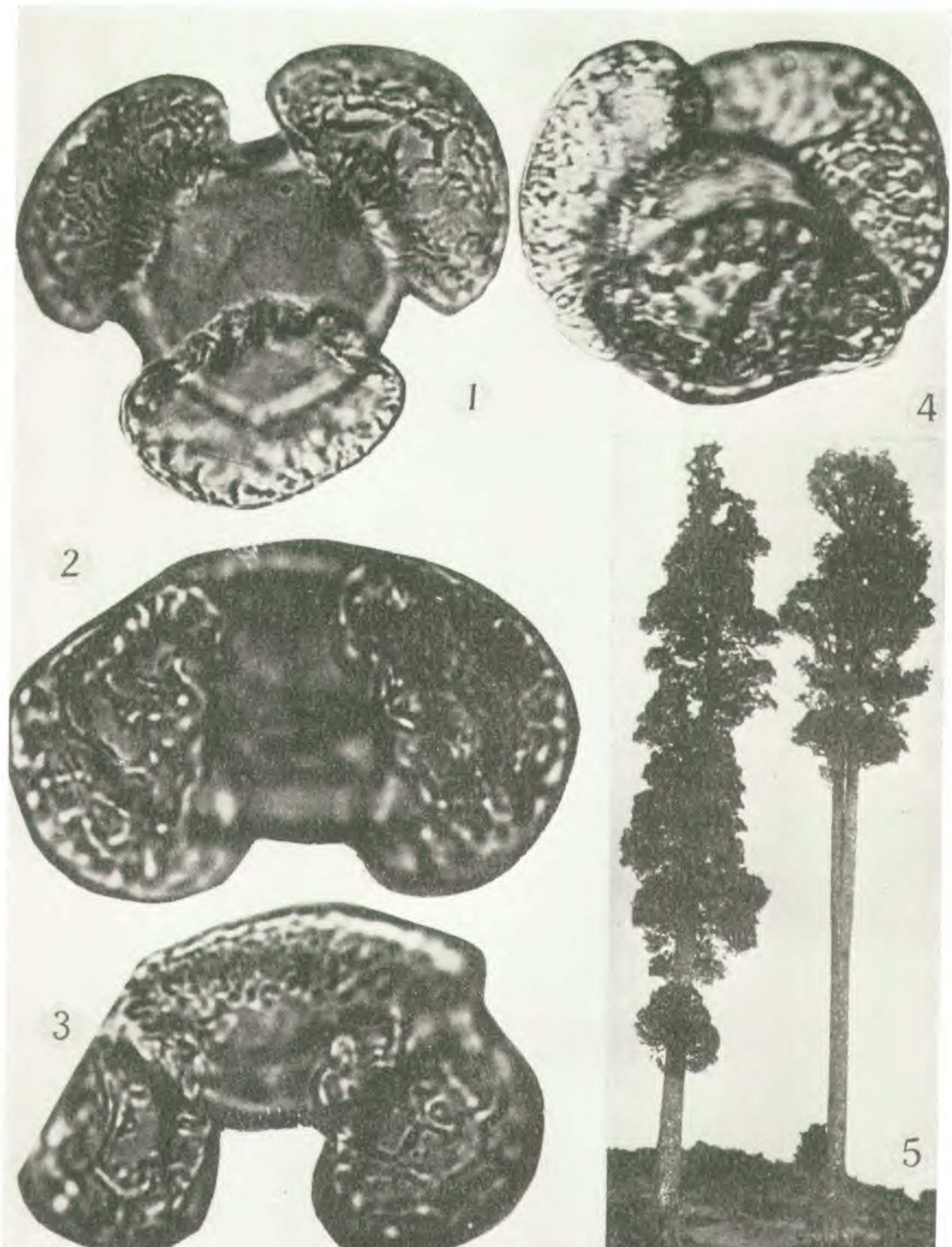
EXPLANATION OF PLATES

PLATE I

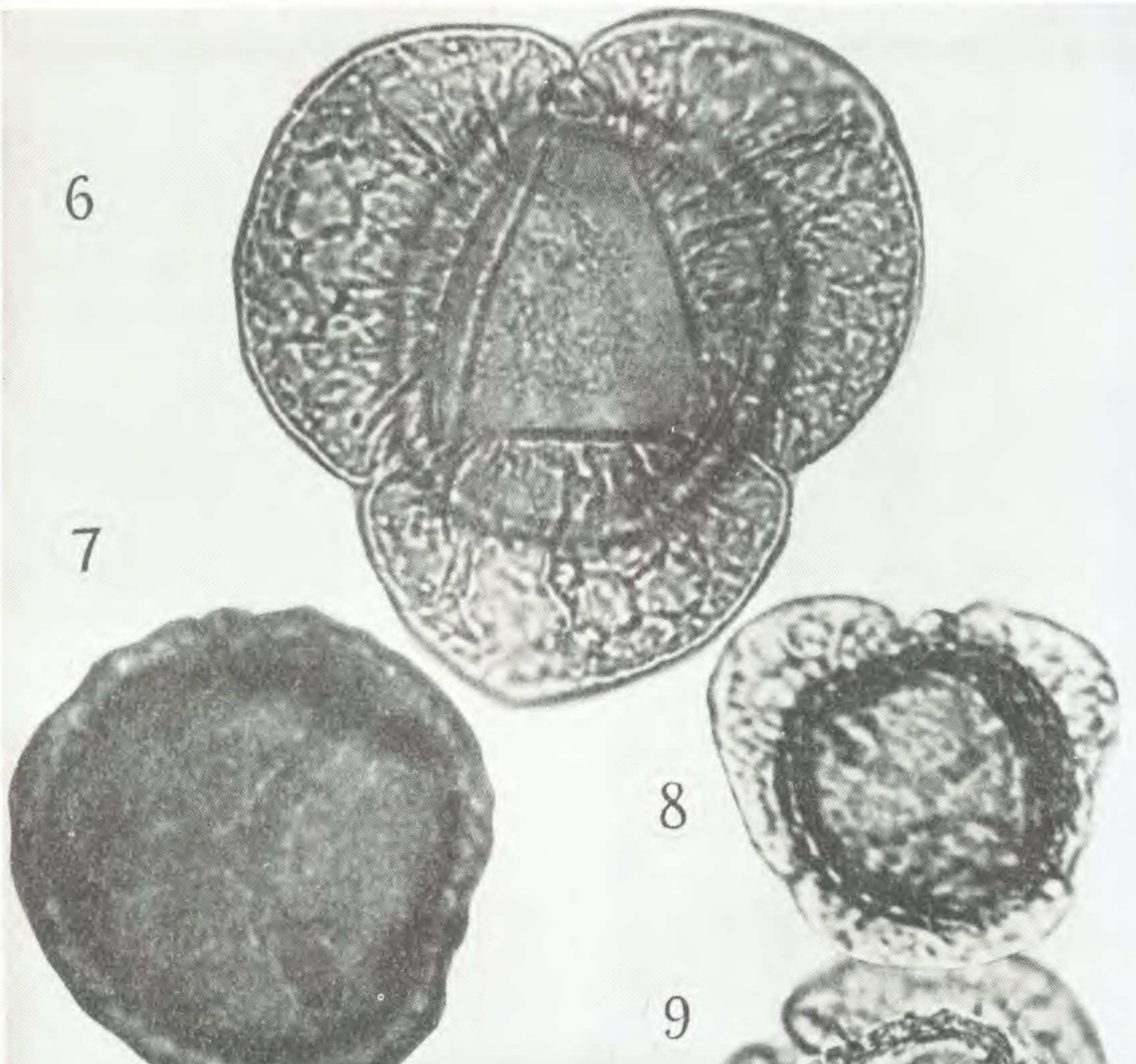
FIGS. 1–5. *Acmopyle* and *Podocarpus*. FIGS. 1–3. Photomicrographs of pollen grains of *Acmopyle pancheri*. 1, Trisaccate grain, 62μ, showing the symmetric and widely spaced sacs, the lowest being turned inward slightly toward the germinal area or "furrow." 2, Disaccate grain, 69μ, showing distal or "furrow" side of grain. 3, Disaccate grain, 69μ, in lateral view showing the puffed sacs on their narrow bases, their slight projection beyond the body of the grain, and their open reticulation of the sacs [Material: *De Laubenfels P130*; pollen preparation, p5 (acetolysed)]. FIG. 4. Photomicrograph of pollen grain of *Podocarpus dacrydioides*. Normal grain in slightly oblique view, the sacs crowd closely together above the rounded "furrow" area; 65μ. [Material: *L. M. & E. A. Cranwell*; pollen preparation S768 (acetolysed)]. FIG. 5. Very old trees of *Podocarpus dacrydioides* ("Kahikatea") isolated after felling of forest around them; King Country, New Zealand. Photographs by author.

PLATE II

FIGS. 6–11. Photomicrographs of pollen grains of *Podocarpus dacrydioides*. 6, Distal view of normal grain (possibly not fully mature), 65μ, showing attachment of the wide bases of the sacs on the large triangular "furrow" area. 7, 8, Young grains, 46 μ, showing the broad triradiate scars on their cap (proximal) side — bladders have been trimmed away in fig. 7 leaving only body or corpus of grain. 9, 10, Aberrant grains with open wound-like scars. 11, Normal grain overlapping an aberrant one (10), both about 70 μ.



Cranwell, Coniferous Pollen Types, I



CRANWELL, CONIFEROUS POLLEN TYPES, I